

The Morphology and Anatomy of Styles in Viciae (Leguminosae)

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To find useful characters contributing to clarify phylogenetic relationships among the species of Viciae (Leguminosae), comparative morphology and anatomy of styles of the genera *Lathyrus*, *Lens*, *Pisum* and *Vicia* were studied. Eight types of styles in transectional outlines at the pollen brush region (when adaxial surfaces face downwards) were distinguished. These types are 1, circular; 2, dorsally compressed oval; 3, laterally compressed oval; 4, inverted triangular; 5, triangular with elongation of lateral sides; 6, dorsally compressed oval with elongation of lateral sides; 7, segmental (chard faces downwards) with elongation of lateral sides; and 8, V-shaped with elongated margins meeting abaxially. The inverted triangular type is presumed to be apomorphic against the circular type according to the out-group rule. This type was observed only in the species of *Vicia* which, at the same time, always has an abaxially tufted pollen brush. These *Vicia* species found to have other two apomorphic characters, i.e., a styler canal runs through the extremely adaxial side in the pollen brush region against through almost central, and the style is club-shaped against tapered. These features may support monophyly of these *Vicia* species.

Introduction

The genus *Vicia* is one of five genera, i.e., *Lathyrus*, *Lens*, *Pisum*, *Vavilovia*, and *Vicia*, of tribe Viciae (Leguminosae) and is composed of about 140 species (Kupicha 1981b). In the genus *Vicia*, 53 species have dorsally compressed and abaxially tufted styles (Kupicha 1976). The characteristics of styler hair which corresponds with pollen brush in the sensu of Lavin and Delgado (1990) was considered to have polyphyletic origin by Kupicha (1976) based on sporadic distribution of the species with such pollen brush in Eurasia, North America, and South America, and on lack of features correlated with it. Then, these species were classified into two subgenera in Kupicha's infrageneric system of *Vicia*. However, Endo and Ohashi (1995, 1996a)

found two synapomorphic characters of these species as follows: 1, V-shaped boundaries between stigma and style; and 2, granular interstitia of pollen grains. They presumed monophyly of the abaxially tufted pollen brush pattern.

Whether is the styler feature monophyletic or polyphyletic? In the present study, to solve the problem, we examined styler shapes and styler internal structures of *Vicia* species together with the species of the other genera of Viciae, because the tribe Viciae was presumed to be monophyletic (Endo and Ohashi 1997) but the monophyly of the genus *Vicia* is uncertain (Endo and Ohashi 1995, 1996a).

The styler morphology has been regarded as one of the most important characters for considering phylogenetic relationships among

the species of the tribe Viciae (Kupicha 1973, 1976, 1977, 1981b, 1983; Gunn and Kluve 1976; Lassetter and Gunn 1979; Lavin and Delgado 1990; Endo and Ohashi 1995, 1996b, 1997). In the tribe, following styler types were recognized by Kupicha (1976, 1981b): 1, terete and evenly pubescent; 2, dorsally compressed and evenly pubescent; 3, dorsally compressed and abaxially tufted; 4, laterally compressed; 5, dorsally compressed and adaxially pubescent; and 6, dorsally compressed, longitudinally folded with margins meeting abaxially, and adaxially pubescent. Styler types of most of *Vicia* species were 1–4, those of *Lathyrus* and *Lens* were 5, and those of *Pisum* and *Vavilovia* were 6 (Kupicha 1976, 1981b).

In the present study, to recognize the styler characteristics of Viciae in detail, we observe development of styles, outlines of mature styles by making serial transections of styles, and anatomical characters of the styles. About the anatomical characters, we can get no data from existing reports.

To discuss the evolution of styler characteristics observed in Viciae, we compare the features with those of the sister-group of Viciae, i.e., tribe Cicereae (Endo and Ohashi 1996c).

Materials and Methods

In the present observation, 61 individuals of 37 species of the tribe Viciae were examined and their voucher specimens are listed in Table 1. These species are the representative ones of the genera *Lathyrus*, *Lens*, *Pisum*, and *Vicia*, and include all known styler outer morphological types of Viciae.

The transectional shapes of styles were observed with light microscope (LM). These styles were fixed with 50% aqueous ethanol: formalin: acetic acid in 17: 2: 1 proportions (FAA). For observations of serial transections with LM, these materials were dehydrated in an n-butyl alcohol series and embedded in

“Hist-Paraffin” (m.p. 56–58°C, Wako Pure Chemical Industries, Ltd., Japan). After embedding, styles were cut into serial transections with 4 μ m thickness. The sections were stained with safranin and fast green FCF, and mounted with “Diatex” (AB Wilh. Becker, Sweden). For observations of styler shapes with scanning electron microscope (SEM), the materials suspended in FAA were dehydrated with an ethanol series and then removed to an isoamyl-acetate pool. The materials were criticalpoint dried and sputtercoated with platinum-palladium (Pt-Pd).

Results

Pollen brush patterns – Four patterns of pollen brush appearance at immature stage of styles were observed. They are 1, pollen brush appears at the adaxial surfaces (Fig. 1); 2, appears abaxially (Endo and Ohashi 1996b); 3, appears abaxially without just below stigma (Endo and Ohashi 1995); and 4, appears all-round styles (Endo and Ohashi 1995). The pattern-1 was observed in the species with adaxially hairy styles, the pattern-2 and -3 in the species with abaxially longer hairy styles, and the pattern-4 in the species with evenly hairy styles.

Anatomical features – A styler canal usually appears in the center of the style at the base (Fig. 2). The canal becomes narrow toward the apex (Figs. 3, 4) and closes just below the stigma (Fig. 5). In pollen brush regions, styler canals are situated somewhat adaxially, and the width of the abaxial layers is about twice of that of adaxial layers (Fig. 4). The styler canals, of *Vicia* species with abaxially tufted pollen brush (Fig. 6) and of *Pisum sativum* (Fig. 7), are found on the extremely adaxial side of styler transections and the abaxial layers of those styles are much more developed than the adaxial layers. The widths of the abaxial layers appear to be more than three times that of the adaxial layers.

Table 1. List of species examined and their voucher specimens

Species and collection site	Voucher specimen ^a
<i>Lathyrus alpestris</i> (Waldst. & Kit.) Kit. CULT. ^b : seeds obtained from Biowissenschaften der Karl-Marx-Univ., Germany	Y. Endo 3100 (CBM)
<i>L. aphaca</i> L. CULT.: seeds obtained from Bot. Gart. der Univ. Untere Karspule, Göttingen, Germany	Y. Endo 3099 (CBM)
<i>L. cicera</i> L. CULT.: seeds obtained from Jard. Bot. Univ. de Caen, France	Y. Endo 2837 (CBM)
<i>L. davidii</i> Hance JAPAN. Aichi Pref., Kokonoka-machi JAPAN. Nagano Pref., Karuizawa KOREA	H. Hoshi in 1982 (TUS) Y. Endo 3090 (CBM) Y. Endo 2888 (CBM)
<i>L. hirsutus</i> L. CULT.: seeds obtained from Hortus Botanicus Nationalis Belgii	Y. Endo 2845 (CBM)
<i>L. japonicus</i> Willd. JAPAN. Chiba Pref., Kujukuri	Y. Endo 3098 (CBM)
<i>L. latifolius</i> L. JAPAN. Chiba Pref.	No voucher specimen
<i>L. magellanicus</i> Lam. CHILE. Magallanes, Puerto Natales, mountain slope	Y. Endo 3032 (CBM)
<i>L. pratensis</i> L. CULT.: seeds origin unknown RUSSIA. Akademgorodok	Y. Endo 3097 (CBM) M. Wakabayashi et al. in 1992 (CBM, MAK)
<i>Lens culinalis</i> Medicus CULT.: seeds obtained from Toronto, Canada CULT.: seeds obtained from Bot. Gard. of the Univ. Nijmegen, Netherlands CULT.: seeds obtained from Bot. Garten der Univ. Zürich, Switzerland	Y. Endo 3102 (CBM) Y. Endo 3106 (CBM) Y. Endo 3107 (CBM)
<i>Pisum sativum</i> L. CULT.: seeds obtained from Hort. Bot. Hauniensis, Denmark JAPAN. Chiba Pref., Ichihara-shi (cultivated)	Y. Endo 2841 (CBM) Y. Endo et al. in 1992 (CBM)
<i>Vicia americana</i> Mühl. ex Labill var. <i>sinensis</i> Gunn CULT.: seeds obtained from Beijin Bot. Gard., China CHINA. Harbin	Y. Endo 2847 (CBM) R. Li 92 (HANU)
<i>V. amoena</i> Fisch. JAPAN. Miyagi Pref., Sendai-shi, Aobadai JAPAN. Yamanashi Pref., Mt. Fuji Russia. Akademgorodok	Y. Endo 586 (TUS) Y. Endo 2918 (CBM) M. Wakabayashi et al. in 1992 (MAK)

- V. amurensis* Oetting.
 JAPAN. Akita Pref., Oga-shi, Goriai Y. Endo 471 (TUS)
 JAPAN. Chiba Pref., Katsuura-shi Y. Endo 2872 (CBM)
 JAPAN. Yamanashi Pref., Mt. Fuji Y. Endo 3081 (CBM)
- V. angustifolia* L.
 CHILE. Isl. Chiloe Y. Endo 3006 (CBM, SGO)
 JAPAN. Chiba Pref., Chiba-shi, Aoba-cho Y. Endo 2887 (CBM)
 JAPAN. Miyagi Pref., Shiroishi-shi H. Sakai et al. in 1983 (TUS)
- V. benghalensis* L.
 CHILE. side of river Biobio Y. Endo 2997 (CBM, SGO)
 CULT.: seeds obtained from Hort. Bot. Coimbra, Y. Endo in 1985 (TUS)
 Portugal
- V. bifolia* Nakai
 JAPAN. Saitama Pref., Chichibu-gun Y. Endo 589 (TUS)
 CULT.: originated from Japan, Tokyo Pref., Y. Endo 2384 (TUS)
 Hachioji-shi
- V. bithynica* (L.) L.
 CULT.: seeds obtained from Jard. Bot. de Barcelona, Y. Endo 2830 (CBM)
 Spain
 CULT.: seeds obtained from Hortus Botanicus Y. Endo 2835 (CBM)
 Coimbra, Portugal
- V. cracca* L.
 JAPAN. Chiba Pref., Inba-gun, Inba-mura K. Oono in 1990 (CBM)
 JAPAN. Kumamoto Pref., Aso-gun Y. Endo 782 (TUS)
 JAPAN. Miyagi pref., Motoyoshi-gun H. Ohashi et al. in 1986 (TUS)
 JAPAN. Nagano Pref., Okaya-shi Y. Mikanagi in 1992 (CBM)
 JAPAN. Yamagata Pref., Murayama-shi Y. Endo 383 (TUS)
 RUSSIA. Akademgorodok M. Wakabayashi et al. 9280072
 (CBM, MAK)
- V. dichroantha* Diels
 CHINA. N.W. Yunnan H. Sun in 1995 (CBM)
- V. dumetorum* L.
 CULT.: seeds obtained from Biowissenschaften der Y. Endo 2886 (CBM)
 Karl-Marx-Univ., Germany
 CULT.: seeds obtained from Hillesthög AB, Sweden Y. Endo 2346 (TUS)
- V. faba* L.
 CULT.: seeds obtained from Univ. Bot. Gard., Y. Endo 2839 (CBM)
 Oxford, England
- V. grandiflora* Scop.
 CULT.: seeds obtained from Bot. Gart. Y. Endo 2824 (CBM)
 der Technischen Univ., Dresden, Germany
- V. hybrida* L.
 CULT.: seeds obtained from Jard. Bot., Y. Endo 2834 (CBM)
 Univ. de Caen, France
- V. japonica* A. Gray
 CULT.: transplantation from Miura Peninsula, Y. Tateishi 1947 (TI)
 Kanagawa Pref., Japan
 JAPAN. Akita Pref., Oga-shi Y. Endo 469 (TUS)
 JAPAN. Hokkaido Pref., Isl. Rebun-to Y. Endo 3083 (CBM)

<i>V. lathyroides</i> L.	
CULT.: seeds obtained from Bot. Gart., Berlin-Dahlem, Germany	Y. Endo 2842 (CBM)
<i>V. lutea</i> L.	
CULT.: seeds obtained from Bot. Gard., Univ. of Coimbra, Portugal	Y. Endo 2457 (TUS)
<i>V. magellanica</i> Hook. f.	
CHILE. Magallanes, Puerto Natales	Y. Endo 3037 (CBM)
<i>V. michauxii</i> Sprengel	
CULT.: seeds obtained from Hort. Bot. Hauniensis, Denmark	Y. Endo 2843 (CBM)
<i>V. narbonensis</i> L.	
CULT.: seeds obtained from Hort. Bot. Univ. Iassiensis, Romania	Y. Endo 2832 (CBM)
<i>V. nummularia</i> Hand.-Mazz.	
CHINA. N.W. Yunnan	H. Sun in 1995 (CBM)
<i>V. oroboides</i> Wulfen	
CULT.: seeds obtained from Neuer Bot. Gart. der Univ., Göttingen, Germany	Y. Endo 2845 (CBM)
<i>V. pannonica</i> Crantz	
CULT.: seeds obtained from Hort. Bot. Hauniensis, Denmark	Y. Endo 2831 (CBM)
<i>V. peregrina</i> L.	
CULT.: seeds obtained from Hort. Bot. Hauniensis, Denmark	Y. Endo 2827 (CBM)
<i>V. sepium</i> L.	
CULT.: seeds obtained from Hillesthög AB, Sweden	Y. Endo 2770 (TUS)
<i>V. venosa</i> (Willd.) Max. var. <i>cuspidata</i> Max.	
JAPAN. Toyama Pref., Unazuki-machi	Y. Endo 2423 (TUS)
<i>V. villosa</i> Roth subsp. <i>varia</i> (Host.) Corb.	
JAPAN. Yamagata Pref., Murayama-shi, Goten	Y. Endo 382 (TUS)

^aHerbarium abbreviations: CBM, Herbarium, Natural History Museum and Institute, Chiba, Japan; HANU, Herbarium, Department of Biology, Harbin Normal University, China; MAK, Makino Herbarium, Tokyo Metropolitan University, Japan; SGO, Herbario of Sección Botánica, Museo Nacional de Historia Natural, Chile; TI, Herbarium, Botanical Gardens, University of Tokyo, Japan; TUS, Herbarium, Biological Institute, Faculty of Science, Tohoku University, Japan.

^bCULT. = Cultivated in green house.

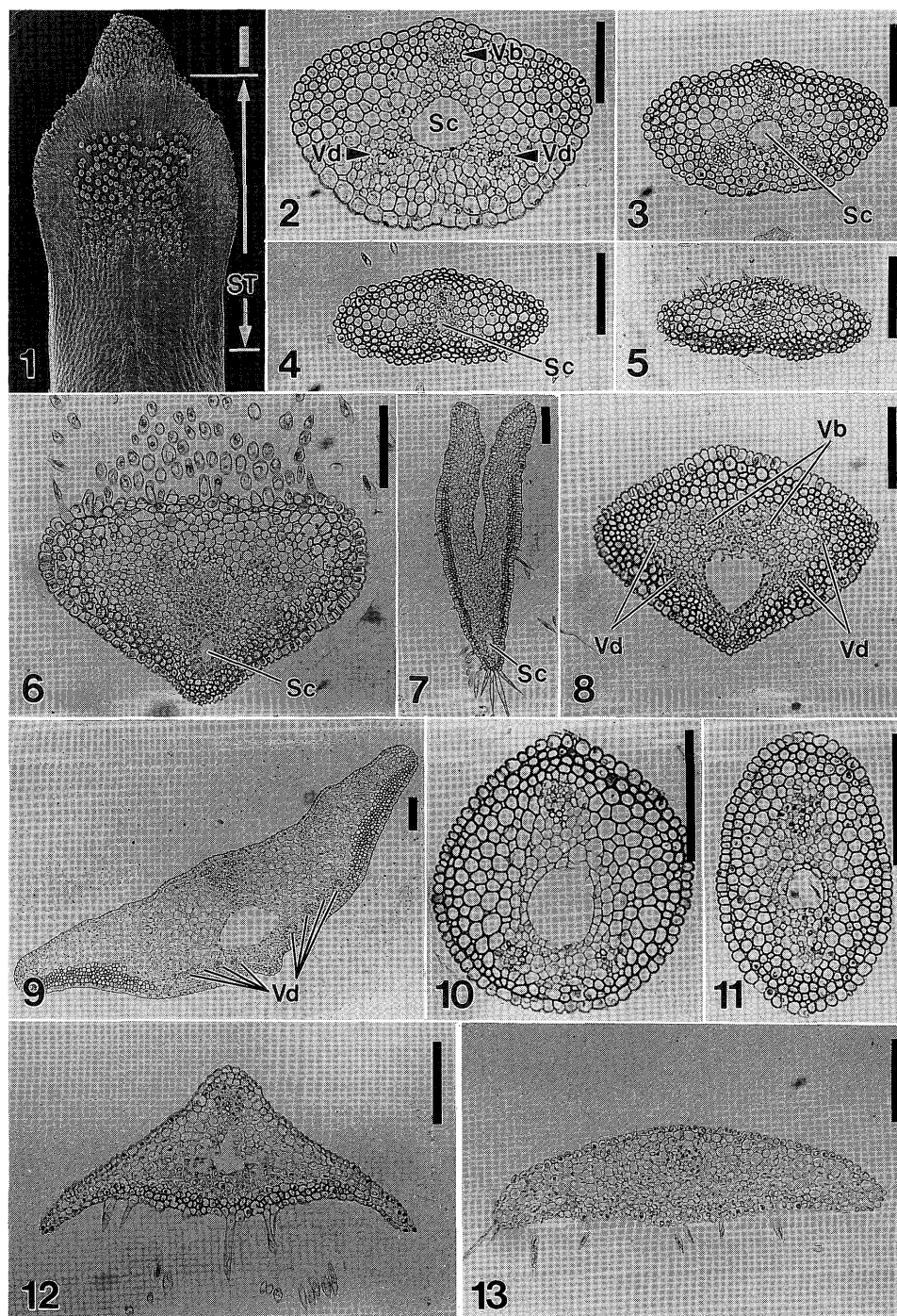
The styler canal is usually surrounded by three vascular bundles (Fig. 2); two of them are situated adaxially and the other abaxially. In some *Vicia* species with abaxially tufted styles, four adaxial vascular bundles are observed in the basal region of a style (Fig. 8).

Adaxial bundles are about eight in *Pisum sativum* (Fig. 9). On the other hand, two abaxial vascular bundles were observed at a level close to the pollen brush region in *Vicia grandiflora* (Fig. 8).

Stylar shapes – Eight types of stylar shapes

were recognized when adaxial surface face downwards. They are 1, tapering and terete styles with circular transectional outline (Fig. 10); 2, tapering and dorsally compressed styles

with oval outline (Fig. 3); 3, tapering and laterally compressed styles with oval outline (Fig. 11); 4, club-shaped (Fig. 14), i.e., becoming thicker from base to the pollen brush re-



gion, and having inverted-triangular transectional outlines at pollen brush region (Fig. 6); 5, spatulate (Fig. 1), i.e., becoming wider from base to the pollen brush region by elongation of lateral sides, and dorsally compressed styles with triangular outline (Fig. 12) at pollen brush regions; 6, spatulate and with oval outline (Fig. 13) at pollen brush regions; 7, spatulate and having segmental outline with chord facing downwards at pollen brush region; and 8, spatulate and folded longitudinally at pollen brush region with V-shaped outline (Fig. 7). Furthermore, the type-4 and -5 are subdivided according to the presence or absence of necks just below stigma (Fig. 15).

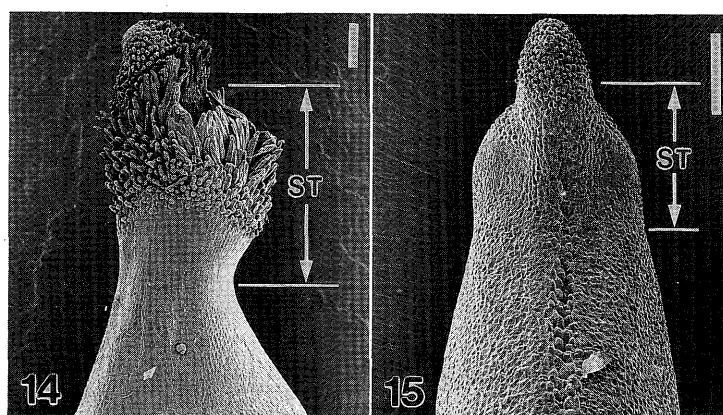
The styler features of the species examined

were summarized in Table 2.

Discussion and Conclusion

Polarity of transformations of styler characters – The tribe Viciae is considered to be monophyletic because of its sharing several apomorphic characters (Endo and Ohashi 1997). Its sister group is presumed to be the tribe Cicereae (Endo and Ohashi 1997). Therefore, the character states of the tribe Viciae same as observed in the species of Cicereae are presumed to be plesiomorphic by the out-group rule (Wiley 1981).

According to Shivanna and Owens (1989), and Kupicha (1981a), the styler features of Cicereae are glabrous, tapering, having circu-



Figs. 14, 15. SEM photos of styler surfaces of *Vicia hybrida* (14) and *V. magellanica* (15) at immature stage. 14. Side view. 15. Adaxial view. Scale bars = 0.1 mm. Abbreviation: ST, style. Voucher specimens: 14, Y. Endo 2834; 15, Y. Endo 3037.

Figs. 1–13. The SEM photo of styler surface (1) and LM photos of styler transections (2–13) of eight species of Viciae. 1. *Lathyrus davidii*. 2–5. *Vicia bifolia*. 6, 8. *V. grandiflora*. 7, 9. *Pisum sativum*. 10. *Vicia amurensis*. 11. *V. benghalensis*. 12. *Lathyrus aphaca*. 13. *L. japonicus*. 1. Adaxial surface of immature style. 2, 9. Transections of mature styles at the base. 3, 8, 10, 11. Transections just below hairy regions. 4, 6, 7, 12, 13. Transections at hairy regions. 5. Transection just below stigma. Adaxial surfaces face downwards. Scale bars = 0.1 mm. Abbreviations: Sc, styler canal; ST, style; Vb, abaxial styler vascular bundle; Vd, adaxial styler vascular bundle. Voucher specimens: 1, Y. Endo 3090; 2–5, Y. Endo 589; 6, 8, Y. Endo 2824; 7, 9, Y. Endo 2841; 10, Y. Endo 471; 11, Y. Endo in 1985; 12, Y. Endo 3099; 13, Y. Endo 3098.

Table 2. Distribution of styler characteristics in Viciae

Species	Characteristics ^a						
	1	2	3	4	5	6	7
<i>Vicia amoena</i>	al ^d	Al ^d	do ^b	CE	2	t	a
<i>V. bifolia</i>	al ^d	Al ^d	do ^d	CE	2	t	a
<i>V. japonica</i>	al ^d	Al ^d	do ^b	CE	2	t	a
<i>V. venosa</i> var. <i>cuspidata</i>	al ^d	Al ^d	do ^d	CE	2	t	a
<i>V. amurensis</i>	ab ^d	Ab ^d	c ^b	CE	2	t	a
<i>V. dichroantha</i>	ab ^d	Ab ^d	c ^d	CE	2	t	a
<i>V. nummularia</i>	ab ^d	Ab ^d	c ^d	CE	2	t	a
<i>V. benghalensis</i>	ab	Ab	lo	CE	2	t	a
<i>V. cracca</i>	ab	Ab	lo ^b	CE	2	t	a
<i>V. villosa</i> subsp. <i>varia</i>	ab	Ab	lo	CE	2	t	a
<i>V. dumetorum</i>	abt ^c	Ab ^c	it	AD	4	cl	a
<i>V. bithynica</i>	abtg ^c	Ab ^c	it	AD	4	cl	p ^b
<i>V. grandiflora</i>	abtg ^c	Ab ^c	it	AD	4	cl	p
<i>V. angustifolia</i>	abtg ^c	Ab ^c	it	AD	2	cl	p
<i>V. lutea</i>	abtg ^c	Ab ^c	it	AD	2	cl	p
<i>V. magellanica</i>	abtg	Ab	it	AD	2	cl	p
<i>V. peregrina</i>	abtg ^c	Ab ^c	it	AD	2	cl	p ^b
<i>V. americana</i> var. <i>sinensis</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. faba</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. hybrida</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. lathyroides</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. michauxii</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. narbonensis</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. oroboides</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. pannonica</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>V. sepium</i>	abtg ^c	Ab ^c	it	AD	2	cl	a
<i>Lathyrus alpestris</i>	ad	Ad	tl	CE	2	sp	a
<i>L. aphaca</i>	ad	Ad	tl	CE	2	sp	a
<i>L. davidii</i>	ad	Ad	tl	CE	2	sp	a
<i>L. cicera</i>	ad	Ad	s	CE	2	sp	a
<i>L. latifolius</i>	ad	Ad	s	CE	2	sp	a
<i>L. pratensis</i>	ad	Ad	s	CE	2	sp	a
<i>L. japonicus</i>	ad	Ad	dl	CE	2	sp	a
<i>L. magellanicus</i>	ad	Ad	dl	CE	2	sp	a
<i>L. hirsutus</i>	ad	Ad	dl	CE	2	sp	p
<i>Lens culinalis</i>	ad	Ad	tl	CE	2	sp	a
<i>Pisum sativum</i>	ad	Ad	v	AD	8	sp*	a

^aCharacteristics:

1, styler hair pattern; ab = hairy all round and abaxially longer, abt = abaxially longer and tufted without glabrous spot, abtg = abaxially longer and tufted with glabrous spot just below stigma, ad = adaxially pubescent, al = evenly hairy all round.

2, styler hair appearance; Ab = appeared abaxially, Ad = adaxially, Al = all round.

3, stylar transectional outlines at the pollen brush region (when adaxial surface face downwards); c = circular, dl = dorsally compressed oval with elongation of lateral sides, do = dorsally compressed oval, it = inverted triangular, lo = laterally compressed oval, s = segmental (chard faces downwards) with elongation of lateral sides, tl = triangular with elongation of lateral sides, v = V-shaped.

4, position of stylar canal; AD = adaxially, CE = almost centrally.

5, number of adaxial stylar vascular bundles.

6, stylar shapes; cl = club-shaped, sp = spatulate (sp* = spatulate and folded longitudinally with margins meeting abaxially), t = tapering.

7, neck just below stigma; a = absent, p = present.

^bData from Endo (1994).

^cData from Endo and Ohashi (1995).

^dData from Endo and Ohashi (1996b).

lar transectional outlines, and having stylar canal positioned almost centrally. Therefore, the polarities of character transformations in Viciae are able to be determined as follows:

1, stylar transectional outlines; circular → laterally compressed oval, dorsally compressed oval, inverted triangular, triangular with elongation of lateral sides, dorsally compressed oval with elongation of lateral sides, segmental with elongation of lateral sides, or V-shaped;

2, stylar canal position; almost centrally positioned → adaxially;

3, stylar shapes; tapering → spatulate or club-shaped;

4, stylar shapes; sessile → having neck just below stigma.

Implications of stylar characters for consideration of phylogenetic relationships among the Viciae species – The *Vicia* species with an abaxially tufted pollen brush are found to share three apomorphic stylar characters in Viciae as follows:

1, a stylar transectional outline in the pollen brush region is inverted triangular;

2, a stylar canal runs extremely adaxially in the pollen brush region;

3, the style is thicker in the pollen brush region than the basal region; i.e., club-shaped.

These species are already known to have other apomorphies, i.e., V-shaped boundaries

between stigma and style (Endo and Ohashi 1995), and granular interstices of pollen grains (Endo and Ohashi 1996a). On the other hand, we can not find any apomorphic characters which deny the monophyly of these species in the tribe Viciae. Therefore, we think that the monophyly of these species is supported by the results of the present study. We consider that these species are better rearranged in the infrageneric system.

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遠藤泰彦^a, 大橋広好^b: マメ科ソラマメ連植物の花柱の外部形態と内部構造

マメ科ソラマメ連に属するレンリソウ属, レンズマメ属, エンドウマメ属, ソラマメ属植物37種61個体について, 花柱の外部形態および内部構造を観察し, 各形質について解析を行った. この結果に基づき, ソラマメ連植物の系統関係について議論した.

ソラマメ連植物の花柱は, 花柱有毛部の横断面の形態により, 以下の8タイプが識別できた(花柱の向軸面を下方に配置して記載する): 1, 円形; 2, 背腹方向に偏平な楕円形; 3, 左右方向に偏平な楕円形; 4, 逆三角形; 5, 三角形の左右両端が伸びた形; 6, 背腹方向に偏平な楕円形の左右両端が伸びた形; 7, 弓形(弦部が向軸側に位置する)の左右両端が伸びた形; 8, 左右両端が背軸面で接するV字形. これらのタイプの関係を外群比較法に基づいて考察すると, 円形が原始的な形質状態にあり, 他は派生的な状態にあると考

えられた. これらの中で, タイプ4を持つ種群はすべてソラマメ属に所属し, 花柱上の毛が背軸面で束状にはえるという共通の特徴を持つ. さらに, 本研究の結果から, この種群は以下の2つの特徴を持つことが明らかとなった: 1, 花柱溝が著しく向軸側に寄っている; 2, 花柱が有毛部で肥厚する. これら特徴は, 花柱溝が花柱のほぼ中央を走る場合, そして, 花柱が基部から先端に向かいしだいに細くなる場合に対し, 外群比較法により, それぞれ派生的であると考えられた. これらの派生形質を共有することから, 花柱タイプ4の種群は, ソラマメ連内で単系統であると推定された. しかし, 既存の分類体系では, この種群は多系統であると考えられ, ソラマメ属内で2亜属に分割されている. このため, ソラマメ属の属内の分類体系の再構築が必要であると考えられる.

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